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# Geographical location affects size and materials used in the construction of European Pied Flycatcher (*Ficedula hypoleuca*) nests

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## Abstract

**Background:** Nest construction is a key element of avian reproductive behaviour and the result is often a complex structure that is used for incubation of eggs, which represents an extended phenotype. It is known that nest construction is a plastic behaviour but the extent to which plasticity is observed in a single species with a wide geographical distribution is largely unknown. This study sought to better understand variation in nest size and composition across a very wide geographical area. The hypothesis suggested that location would affect size but not composition of nests of the European Pied Flycatcher (*Ficedula hypoleuca*).

**Methods:** Nests and reproductive data were collected from seventeen study sites, spread over 6° of latitude and 3.3° of longitude on the island of Great Britain. Dimensions of nests were measured before they were deconstructed to determine the masses and types materials used in the outer nest and the cup lining.

**Results:** Geographical variation was observed in base thickness of nests but not many other dimensions. Nests varied in composition but were mainly made of leaf, moss, bark, grass, root and fern. Moss was used more to the north and east of the study area compared with more leaf mass towards the south and west. The species of leaf and bark used in the nests varied between geographical locations. Additionally, the use of leaves or bark from a particular tree species did not reflect the incidence of the tree species in the immediate territory.

**Conclusions:** This study showed that nest composition was affected by geographical location over a wide area. Variation between nests at each location was high and so it was concluded that differences in nest composition reflect individual selection of materials but evidence is such that it remains unclear whether this is deliberate to fulfil a specific role in the nest, or simply opportunistic with birds simply picking up materials with the appropriate characteristics as they find them outside their nestbox.

**Keywords:** Breeding success, *Ficedula hypoleuca*, Latitude, Longitude, Nest composition, Nest size, Nest structure

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## Background

Avian nests are complex structures that represent extended phenotypes and are the place of incubation for all bird species and the site of nestling rearing for many species, particularly passerines (Deeming 2016). Nests exhibit considerable inter-specific (Deeming and Mainwaring 2015; Biddle et al. 2018a) and intra-specific variation in size and composition (Britt and Deeming 2011; Crossman et al. 2011; Briggs and Deeming 2016; Taberner Cerezo and Deeming 2016; Biddle et al. 2018a, b), which can impact upon their functional properties (Biddle et al. 2017, 2018b). For instance, insulatory values of the walls of Common Blackbird (*Turdus merula*) nests significantly correlated with the amount of grass within the cup lining (Mainwaring et al. 2014). Although insulation seemed to be a key role for grass in this case, other studies suggest that materials do not correlate with insulation (e.g., Holland and Shutler 2018). Various species seem to use other materials for different reasons. The inclusion of bryophytes in nest by various species of tit (Paridae) appears to be very selective and not to reflect water absorptive properties as was previously thought (Wesołowski et al. 2002) but rather indicates the degree of support offered by the stems of the different moss species used (Wesołowski and Wierzycholska 2018). Inclusion of white anthropogenic materials in Black Kite (*Milvus migrans*) nests has been interpreted as sign of bird fitness (Sergio et al. 2011). Used cigarette butts incorporated into nests built by House Sparrow (*Passer domesticus*) and House Finch (*Carpodacus mexicanus*) appear to have an anti-parasitic role (Suárez-Rodríguez et al. 2013) despite the potential risks to individual fitness (Suárez-Rodríguez et al. 2017). However, our understanding of the underlying reasons for variation in nest composition is poor and the role for particular materials is not always very clear.

Nests also vary in size and composition according to geographical location with those being constructed at higher latitudes being larger with heavier cup linings or thicker walls (Tiainen et al. 1983; Rohwer and Law 2010; Crossman et al. 2011; Deeming et al. 2012; Mainwaring et al. 2012, 2014). Higher altitudes also affect nest construction (Kern and van Riper 1984). Most of these studies have investigated variation in nest wall composition in relatively few sites, or have not reported the effects of geographical location on the compositional mix of materials used to construct the nest. Whilst we have evidence that latitude has an effect on nest composition, presumably as a response to cooler temperatures (Rohwer and Law 2010; Crossman et al. 2011; Deeming et al. 2012; Mainwaring et al. 2012, 2014), there has yet to be large scale assessment of geographical location on nest materials for one species. Briggs and Deeming (2016) showed

that European Pied Flycatcher (*Ficedula hypoleuca*) (hereafter referred to as the Pied Flycatcher) nests constructed in Lancashire, England were different in composition to nests of the same species described in other studies and constructed during different years in Wales and Spain. Whilst it was not clear what significance these differences had for nest function in this species, it seemed that, contrary to reports of selection of very specific nest materials (e.g. Wesołowski and Wierzycholska 2018), the choice of materials used in nest construction by Pied Flycatchers was opportunistic, as has been observed previously in tit species (Surgey et al. 2012). Pied Flycatchers in Lancashire seemed to select the types of leaves on their availability within the bird's territory immediately outside their nestbox.

Various questions arise from these observations. What is the extent of intra-specific geographical variation in nest composition in a single species? In different locations do birds collecting materials exhibit any preference for a material type, or is it purely opportunistic? Do particular nest materials have a key functional role, for instance in insulation, and so may be unevenly distributed in nests dispersed geographically depending on the prevailing localised climate?

In an attempt to answer at least some of these questions, this study investigated geographical variation in nest size and composition in Pied Flycatchers across the island of Great Britain. Nests collected from seventeen sites, representing 6° of latitude and over 3.3° of longitude, were measured and deconstructed. Given that this species generally nest in woodland where nest cavities are available (Lundberg and Alatalo 1992), and that this habitat is widespread in Great Britain, it was hypothesised that geographical location (as defined by latitude and longitude) would affect nest size but not composition. Nests from cooler northern sites were predicted to be heavier with thicker walls compared to sites further south but no differences in the proportions of nest materials would be observed. In particular, the effect of location on the types and amounts of tree leaves and bark in the nest was investigated and correlated with the incidence of the principal tree species in the flycatchers' territories. Finally, the effects of location on reproductive success was also investigated.

## Methods

A request was published on the website [www.PiedFly.net](http://www.PiedFly.net) for nest recorders to collect Pied Flycatcher nests at the end of the 2016 breeding season. Data requested with each nest included: nest site location name and Ordnance Survey grid references, which were used to read off latitude and longitude from a 1:50,000 scale map, altitude, date of nest start and first egg date (April 1st = day

1), clutch size and brood size, nest outcome and internal nestbox dimensions, from which floor area (cm<sup>2</sup>) was calculated. In addition, participants were asked to identify and count the individual tree species within a 25 m radius of the tree holding the nestbox, which approximates to the size of a Pied Flycatcher territory (Briggs and Deeming 2016). For this data values were available for eleven locations.

Participants were asked to collect the nests after the breeding attempt was completed and place them in individual sealed plastic bags before freezing at  $-20^{\circ}\text{C}$  for 2 days to kill any biting arthropods (Britt and Deeming 2011) before posting the nests to KBB. Thirty-three recorders participated sending 480 nests from 17 different geographical locations in Great Britain. Coordinates given for each location were for the central area of nest collection, which could have a 1–24 km radius. There was a range of over around  $6^{\circ}$  of latitude and over  $3.3^{\circ}$  of longitude with all sites being west of the Greenwich meridian (Table 1).

Once received the nests were re-frozen  $-20^{\circ}\text{C}$  for another 4 days and then air-dried for 14 days in separate plastic trays until dry. Nests were re-sealed in labelled plastic bags and packed into cardboard boxes for storage at room temperature until processing. During this process some of the nests were discarded due to their poor condition having been left too long in a wet nestbox and so had started to rot making the components unrecognisable. Nests from each location were examined separately and, except for Stirlingshire where only five nests

were suitable, twenty of the nests were selected based on their condition. Nests that were largely uncrushed and with a recognisable cup were deemed suitable for measurements and deconstruction. Faeces and the remains of dead young were removed before processing the nests.

Of these nests a subset of 10 per chosen on the basis of the integrity of the cup for measurement of dimensions were all recorded using a steel ruler to the nearest 0.1 cm. Firstly, the external morphology of the nest was quantified by measuring the maximum and minimum diameter of the nest. The height of the external nest was measured at the highest point to the lower edge of the base. The internal cup diameter was measured at what visually appeared to be the maximum and minimum points across the nest cup rim. The depth of the nest was determined by placing the ruler across the rim of the nest and a metal rod was lowered into the cup until it touched the base. The point level with the ruler was marked using a marker pen and this distance was measured. The thickness of the nest wall was measured at the three places where it would have been adjacent to the nestbox wall and excluding the larger packing area of the nest that filled the rest of the box. For each measure a metal rod was pushed through the nest wall until it was felt by a thumb placed within the nest cup and the distance to the nest limit was marked allowing measurement of wall thickness. For base thickness the nest was placed on a metal sheet and the metal rod was pushed through material below the cup base until it made contact with the metal plate. Again the distance was marked on the rod

**Table 1** Details of the locations used in this study showing approximate altitude above sea level, latitude and longitude

Location	Altitude (m)	Latitude ( $^{\circ}\text{N}$ )	Longitude ( $^{\circ}\text{W}$ )	Box area (cm <sup>2</sup> )
Devon	100	50.550	3.817	224
Somerset	140–190	51.183	3.583	210
Glamorganshire	100–200	51.900	3.917	150
Herefordshire	110–250	52.100	2.833	150
Radnorshire	300	52.217	3.500	150
Cardiganshire	270	52.283	3.867	140
Shropshire	150–180	52.467	3.117	165
Montgomeryshire	150–200	52.617	3.283	154
Denbighshire	220–260	52.883	3.200	210
West Yorkshire	200–225	53.950	1.700	165
Lancashire	100–225	54.083	2.600	150
Cumbria	150–280	54.333	2.833	150
North Yorkshire	120–190	54.333	1.083	165
Dumfries and Galloway	30–100	54.833	4.350	154
Durham	200–225	54.950	2.367	165
Northumberland	155	55.233	1.883	154
Stirlingshire	50	56.133	4.417	165

The area of the nestbox base is also included. Sample size was 20 nests per location except for Stirlingshire where only 5 nests were available

and measured. All measurements were made by KBB to minimise error.

The tightly woven inner nest cup could easily be removed from the loosely packed outer nest and the two parts were subsequently deconstructed separately to quantify the various types of materials used in construction based on criteria defined by Briggs and Deeming (2016). All deconstructions were done by KBB. Plant materials were categorised as: bark, fern, grass, leaves, lichen, moss, roots (mainly moss rhizophores), rush (including woodrush), and woody twigs. Animal-derived materials were: feathers, and hair (including wool). Artificial materials, such as plastic, twine, or paper, were also recorded. The dust remaining after the deconstruction process was sieved to isolate any large pieces of material that could be identified. After completion of the deconstruction of the two nest parts the components and dust were weighed on an electronic balance (Pesola PPS200) to the nearest 0.01 g.

During deconstruction it became apparent that different types of leaf and bark seemed to be found in the nests from different locations. To investigate this further, for each nest, the species of tree from which leaf or bark was derived was identified on the basis of shape, colour, texture, type of lenticels, etc. with reference to KBB's specimen collection and to Mitchell (1974). The amounts of materials for each species was then weighed.

### Statistical analysis

Statistical analyses were carried out in Minitab (version 17.0). Spearman rank correlation analysis was used to investigate the associations between the various nest materials identified. One was added to all mass data before being  $\log_{10}$ -transformed prior to analysis. General linear modelling was used to determine the effects of latitude and longitude on nest size and mass, and reproductive data. The part of the nest, i.e. cup or outer nest, was also included in the model as a fixed factor. Box floor area was included in all models as a covariate to control for variation in the basal area of nest boxes used in the different locations (Table 1). Full models were initially run but if the interaction between latitude and longitude was not significant the term was removed and the model was run again. Intraclass correlation coefficients were used to assess similarity between values for each location and were calculated using the ICC package in R (R Core Development Team 2012).

For nest composition Spearman's correlation was used to ascertain which of the main components of a nest showed collinearity. Only a few associations were significantly associated with leaf mass and for those the correlated variable was included as a covariate in an expanded

model that included part of nest part as a fixed factor and latitude and longitude as covariates.

For the different types of leaf and bark general linear modelling was used to determine the effects of latitude and longitude, type of tree and location in the nest, i.e. cup lining or outer nest. The full models was initially run but non-significant higher order interaction terms were removed sequentially and the model was re-run.

For eleven of the locations the number and species of tree was recorded within a 25 m radius of the tree on which the nestbox was attached (Briggs and Deeming 2016). The proportion of oak, birch and beech trees in this area was calculated and compared with the proportion of leaves of each species in the total leaf mass in the nest, and the proportion of bark of each species for the total mass of bark in the nest. Differences between location means for each species were compared using one-sample t-tests against a test mean of zero.

## Results

### Effect of location on nest dimensions

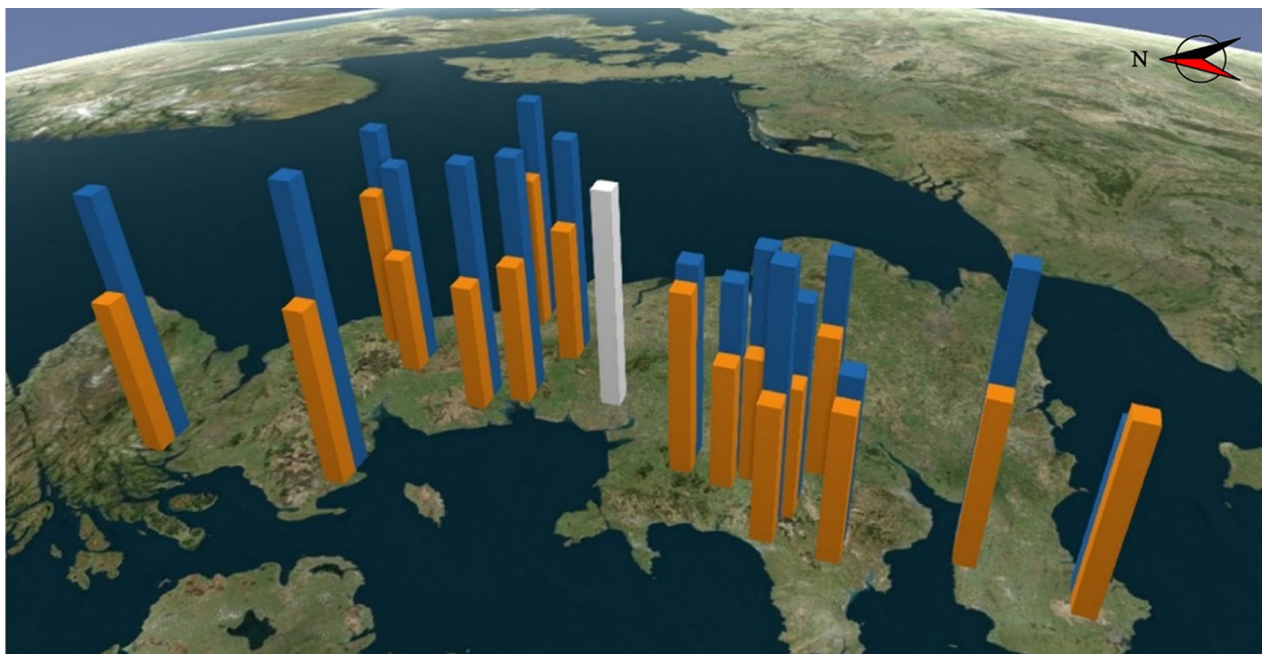
Mean nest dimensions are shown in Additional file 1: Table S1. Latitude and longitude had no significant effect on most of the linear dimensions of the Pied Flycatcher nests (Table 2) with some exceptions. Although differences were small (1–2 mm) average cup diameter was significantly affected by longitude, with wider nests to the east, but was unaffected by latitude (Table 2). By contrast, average wall thickness was significantly affected by latitude but not longitude, with more northerly nests having thicker walls. Base thickness was significantly affected by latitude and longitude with thicker bases towards the north and east (Fig. 1) but there was no significant interaction (Table 2). Total nest mass significantly positively correlated with nest height and

**Table 2 Results of several analyses of covariance to test the effect of latitude and longitude on nest parameters for all of the nest and after it was separated into the outer nest and the cup lining**

	Latitude	Longitude	$R^2$
Mean cup diameter	1.61 (0.207)	5.34 (< 0.001)	11.75
Cup depth	1.27 (0.262)	0.69 (0.406)	3.21
Mean wall thickness	5.84 (0.017)	1.87 (0.174)	22.46
Base thickness	25.69 (< 0.001)	4.86 (0.029)	17.22
Nest height	0.03 (0.866)	1.85 (0.176)	1.93

The model included box area ( $\text{cm}^2$ ) as a covariate to control for variation in box size between locations. All interactions between latitude and longitude were non-significant so the interaction was removed from the model, which was run again. Each parameter was tested individually. Data are presented for five dimensions (shown in Additional file 1: Table S1). Values are  $F$  statistics, with degrees of freedom = 1158 in each case, and  $p$  values in parentheses





**Fig. 1** Mean wall thickness (orange) and base thickness (blue) in the total nest plotted in the appropriate geographical location on the island of Great Britain (facing east) using 3D maps within Microsoft Excel 2016. The view is facing east so the north–south axis is left to right. White scale bar = 2.5 cm. Mean and standard deviation values are reported in Additional file 1: Table S1

base thickness (Spearman's  $\rho_{160} = 0.539$ ,  $p < 0.001$  and  $\rho_{160} = 0.311$ ,  $p < 0.001$ ) but not with mean wall thickness ( $\rho_{160} = 0.130$ ,  $p = 0.099$ ). Intraclass correlation coefficients were low for measures of nest height but moderate to poor for other nest dimensions (Additional file 1: Table S2).

#### Effect of location on nest composition

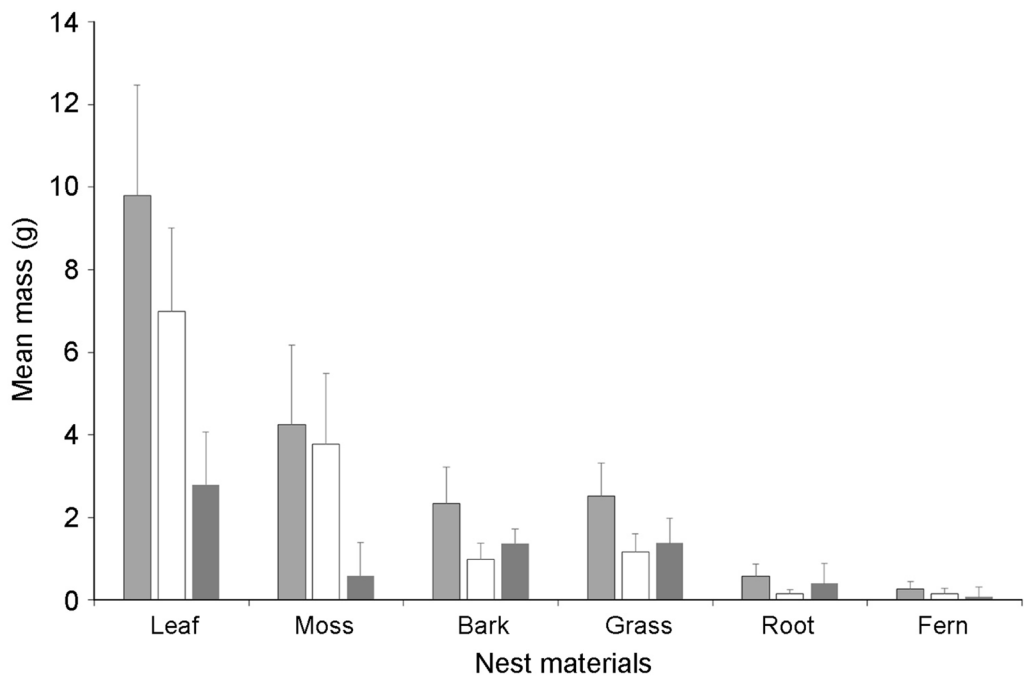
Fourteen different materials were found in the various Pied Flycatcher nests but they were primarily constructed of four main materials: leaves, moss, bark and grass, which all formed at least 2 g of the total nest mass (Fig. 2). Roots and fern formed at least 0.25 g of the total materials but the other materials each formed  $< 0.1$  g of the total nest: woody stems (mean  $\pm$  SD of location means:  $0.081 \pm 0.070$  g), lichen ( $0.013 \pm 0.025$  g), rush ( $0.021 \pm 0.044$  g), and wood chips ( $0.017 \pm 0.023$  g). Hair (derived variously from sheep, deer, cattle, horses, badgers and rabbits) was observed but in small quantities ( $0.071 \pm 0.047$  g), as were feathers ( $0.004 \pm 0.007$  g) and artificial materials ( $0.029 \pm 0.032$  g). There were more leaves, moss and fern in the outer nest compared with the cup lining but bark, grass and roots were found more frequently in the cup lining (Fig. 2). The total nest included an average of 7.1 (SD = 0.6) different materials in each nest with lower averages in the outer nests ( $6.9 \pm 0.6$ ) and the cup lining ( $6.6 \pm 0.5$ ) because some materials were

not used in both parts of the nest. Mean masses for individual nest components in the total nest, outer nest and cup lining are shown in Additional file 1: Table S3, S4 and S5, respectively.

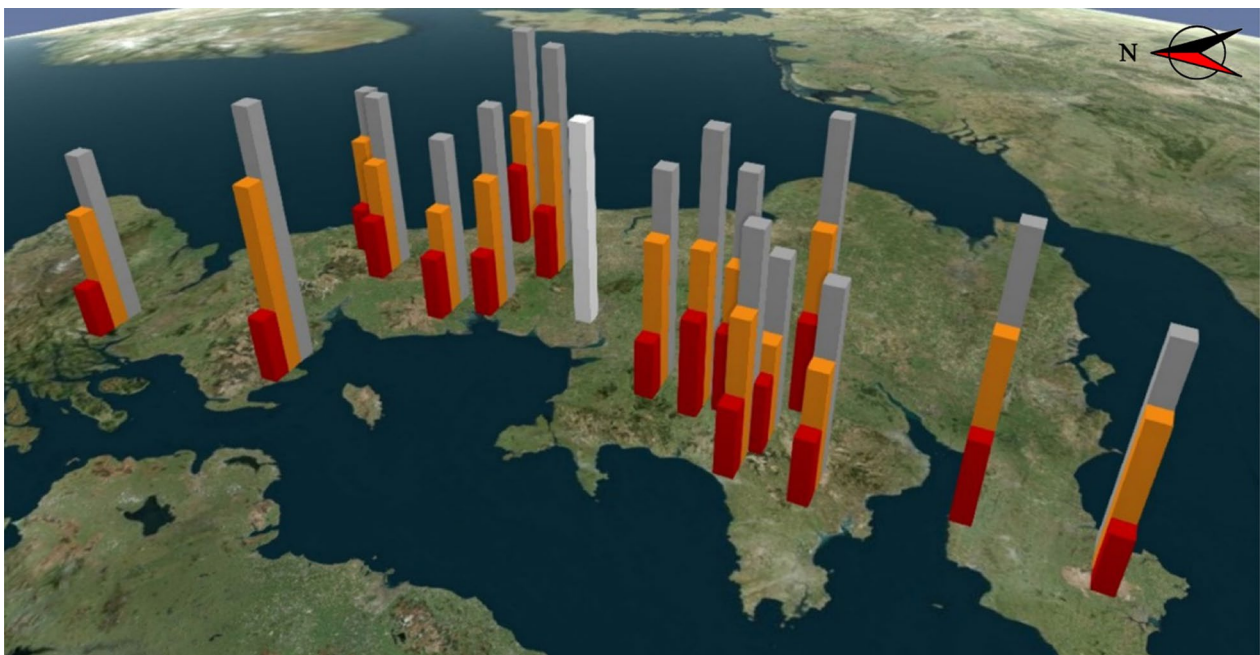
Whilst controlling for variation in box floor area geographical location significantly affected the mass of the entire nest and the outer nest and cup lining separately (Fig. 3, Table 3). There were significant interactions between latitude and longitude with heavier nests tending to be to the south and east although the percentage of variation explained by the model was low (Table 3). Cup mass as a proportion of the total nest mass was significantly affected by latitude and longitude but there was no interaction (Table 3). The cup was a lower proportion of the total nest mass with increasing latitude and further west.

The number of materials used in the whole nest and the outer nest was significantly affected by latitude with more material types occurring with increasing latitude (Table 3). The number of materials used in the cup lining was not affected by latitude. Number of materials used in any part of the nest was not affected by longitude (Table 3).

Spearman rank correlation analysis showed that for the complete nests there was a highly significant negative correlation between mass of leaf and the mass of moss ( $\rho_{323} = -0.372$ ,  $p < 0.001$ ) and positive relationship



**Fig. 2** Mean (+SD) of means for each component calculated for each of the 17 locations for the total nest (light grey), outer nest (white) and cup lining (dark grey)



**Fig. 3** Mean mass of the total nest (grey), outer nest (orange) and cup lining (red) plotted in the appropriate geographical location on the island of Great Britain (facing east) using 3D maps within Microsoft Excel 2016. The view is facing east so the north–south axis is left to right. White scale bar = 20 g. Mean and standard deviation values are reported in Additional file 1: Table S3 and S4

**Table 3 Results of several analyses of covariance to test the effect of latitude and longitude on nest parameters for all of the nest and after it was separated into the outer nest and the cup lining**

Material	Nest part	Latitude	Longitude	Latitude x longitude	R <sup>2</sup>
Total mass (Log <sub>10</sub> )	570.31 (<0.001)	41.54 (<0.001)	37.38 (<0.001)	36.82 (<0.001)	48.9
Materials used	2.98 (0.085)	5.87 (0.016)	3.80 (0.052)	3.95 (0.047)	4.1
Leaf (Log <sub>10</sub> )	316.35 (<0.001)	13.09 (<0.001)	7.48 (0.006)	7.23 (0.007)	35.3
Moss (Log <sub>10</sub> )	288.87 (<0.001)	1.27 (0.261)	3.43 (0.065)	3.64 (0.057)	32.9
Bark (Log <sub>10</sub> )	20.40 (<0.001)	9.11 (0.003)	6.84 (0.009)	6.58 (0.011)	5.9
Grass (Log <sub>10</sub> )	10.01 (0.002)	15.10 (<0.001)	14.91 (<0.001)	14.24 (<0.001)	7.3
Root (Log <sub>10</sub> )	67.27 (<0.001)	30.82 (<0.001)	30.87 (<0.001)	31.50 (<0.001)	15.4
Fern (Log <sub>10</sub> )	35.59 (<0.001)	1.23 (0.268)	1.01 (0.315)	1.02 (0.312)	5.8

The model included box area (cm<sup>2</sup>) as a covariate to control for variation in box size between locations. The parameter in each row was tested individually. Data are presented for the five largest components—analysis for other components are shown in the supplementary materials. Component masses were Log<sub>10</sub>-transformed prior to analysis. Values are *F* statistics, with *p* values in parentheses. Degrees of freedom = 1644 for each factor and covariate

**Table 4 Results of two analyses of covariance to test the effect of latitude and longitude on the mass of leaf in the total nest and the outer nest**

Nest part	Latitude	Longitude	Latitude x longitude	Covariate	R <sup>2</sup>
428.29 (<0.001)	17.92 (<0.001)	12.61 (<0.001)	12.39 (<0.001)	Moss (Log <sub>10</sub> ) 81.43 (<0.001)	42.6
314.33 (<0.001)	11.91 (0.001)	6.75 (0.010)	6.52 (0.011)	Bark (Log <sub>10</sub> ) 1.46 (0.643)	35.4

The model included box area (cm<sup>2</sup>) as a covariate to control for variation in box size between locations. In addition the model included either Log<sub>10</sub> values for moss or bark because these components were shown to significantly correlate with leaf mass. The parameter in each row was tested individually. Component masses were Log<sub>10</sub>-transformed prior to analysis. Values are *F* statistics, with *p* values in parentheses. Degrees of freedom = 1643 for factors and covariates

between leaf mass and barks mass ( $\rho_{323}=0.131$ ,  $p=0.018$ ). Other correlations between the various materials were not significant. Similarly for the outer nest, there were the same patterns (leaf mass and moss mass;  $\rho_{323}=-0.444$ ,  $p<0.001$ ; leaf mass and bark mass:  $\rho_{323}=0.122$ ,  $p=0.028$ ). For the cup lining there was no significant correlations between the five major components (all  $p>0.05$ ) except for a significant negative correlation between moss mass and bark mass ( $\rho_{323}=-0.139$ ,  $p=0.012$ ).

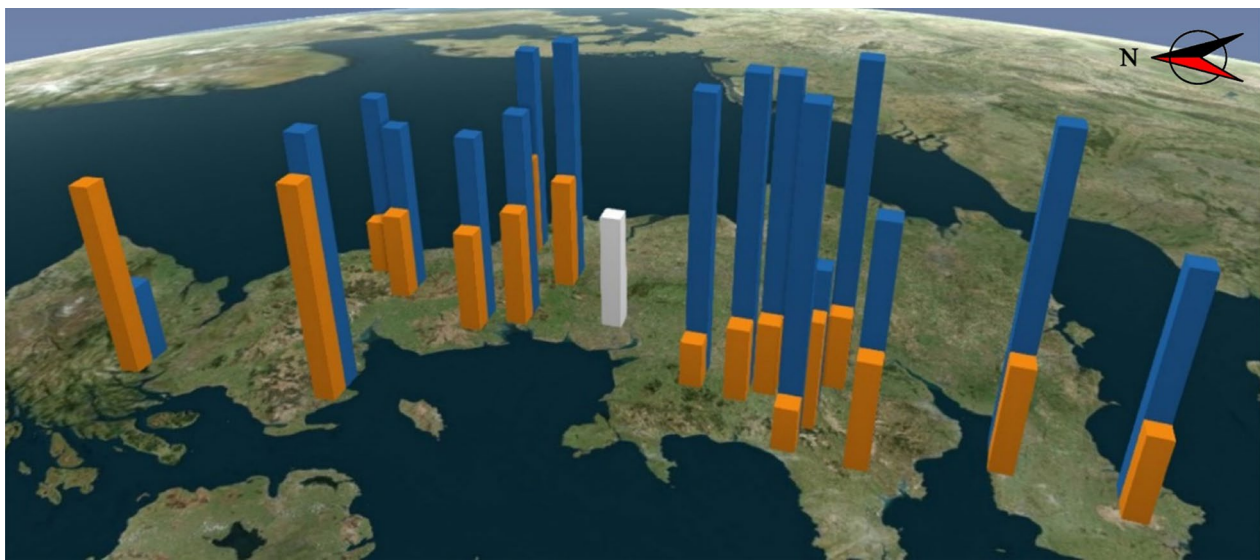
The effects of latitude and longitude on the Log<sub>10</sub>-transformed values for the five main components found in the nests are shown in Table 3. The masses of the nest and its individual components were significantly affected by nest part in all cases but the number of materials was not (Table 3). The mass of leaves in the total nest was significantly affected by latitude and longitude but there was no significant interaction. However, when mass of moss was added as a covariate both latitude and longitude and their interaction significantly affected leaf mass—this was largely due to the significant negative relationship between masses of leaf and moss (Table 4). Generally, more leaves were used in nests to the south and east (Fig. 4). For the outer nest only latitude showed a significant effect on leaf mass (Table 3) but including moss mass as a covariate

revealed a significant effect of latitude and longitude and their interaction (Table 4). Interestingly when bark mass was added as a covariate latitude and longitude affected the leaf mass for the mass of the total nest but only latitude affected the mass of leaf in the outer nest (Table 4). For the cup lining there was also a significant effect of latitude and longitude and their interaction (Table 3) with less leaf mass towards the north and east.

Both latitude and longitude showed significant effects on mass of moss in the whole nest, outer nest and cup lining but with no significant interactions (Fig. 4, Table 3). The amount of bark in the total nest and the cup lining was significantly affected by latitude and longitude and their interaction but was not affected in the outer nest (Table 3).

The amounts of grass and roots in the whole nest or its two component parts, were significantly affected by latitude and longitude and their interaction was also significant (Table 3). By contrast, the amounts of fern in the nest were unaffected by geographical location (Table 3). Geographical location did not generally affect most of the other minor nest components with the exception of rush (Additional file 1: Table S6) but the mean values for this material were less than 0.1 g (Additional file 1: Table S3). It was absent from nests at nine locations and only reached a mean of 0.1 g for nests for Northumberland





**Fig. 4** Mean mass of leaf (blue) and moss (orange) in the total nest plotted in the appropriate geographical location on the island of Great Britain (facing east) using 3D maps within Microsoft Excel 2016. The view is facing east so the north–south axis is left to right. White scale bar = 5 g. Mean and standard deviation values are reported in Additional file 1: Table S3 and S4

(Additional file 1: Table S3 and S6). Nest part did significantly affect the amounts of the minor components with the exception of rush (Additional file 1: Table S6). Intraclass correlation coefficients for all of the mass components were very low ( $<0.018$ ; see Additional file 1: Table S2).

#### Effect of location on utilisation of leaves and bark

The leaves from 15 different species of tree or large shrub were identified in the Pied Flycatcher nests with the commonest species being oak (*Quercus* sp.), birch (*Betula* sp.), beech (*Fagus* sp.), holly (*Ilex* sp.), pine (*Pinus* sp.) and ivy (*Hedera* sp.); leaves from most other tree species were only rarely found. Oak leaves predominated in the nests with greater amounts in the outer nest than the cup lining (Fig. 5a). Inclusion of leaves from other species depended on location; for instance, holly was commonly found in nests from Somerset and beech leaves were common in nests from Cardiganshire. Although no obvious trend was observed for longitude or latitude, there did not seem to be any particular trend in the use of trees from particular species moving from north to south (Fig. 5a), longitude and latitude showed significant interactions with tree species but not nest part. Tree species significantly affected the amounts of leaves in the different parts of the nests and (Table 5). The model explained around 60% of the variation in data (Table 5).

The bark of eight species of tree was observed in the nests. Oak, birch, honeysuckle (*Lonicera* sp.) and pine were common and those of hazel (*Corylus* sp.), cherry

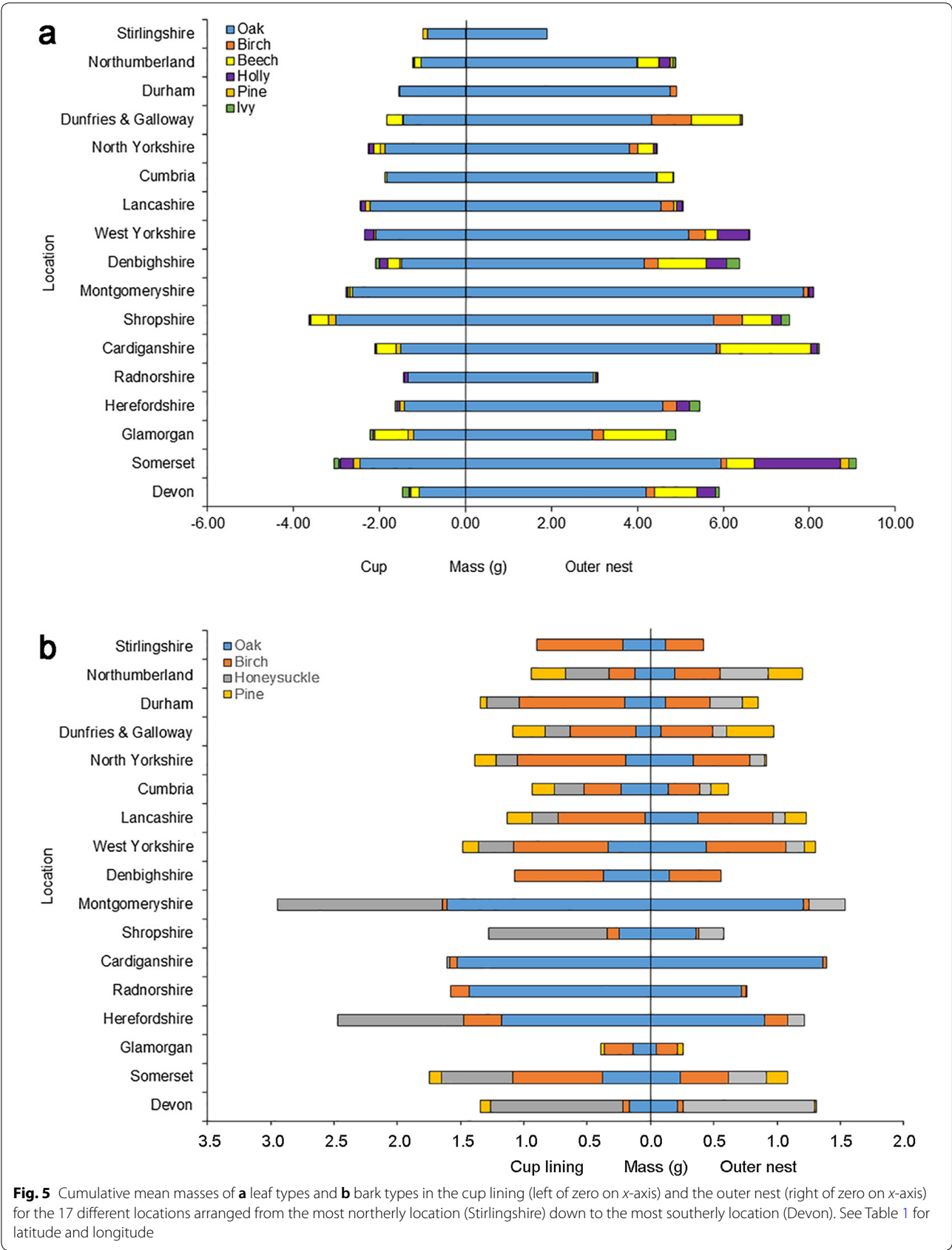
(*Prunus* sp.), lime (*Tilia* sp.) and sycamore (*Acer* sp.) were only rarely found. The amount of bark in the nest was lowest in Glamorgan and highest in Montgomeryshire with more bark generally being found in the cup lining than in the outer nest (Fig. 5b). Nests in Devon used a lot of honeysuckle bark but as the location moved north-eastwards there was a move towards more oak bark (Fig. 5b). However, from Denbighshire northwards there was a switch to more birch bark and increasing amounts of pine bark. The tree species significantly affected the amount of bark on its own and interacting with both longitude and latitude. The same pattern was observed with nest part but to a lesser extent (Table 5). Longitude and latitude were not significant covariates in their own right (Table 5). This model did, however, explain very little (10%) of the variation in the mass of bark.

The proportion of oak trees in a 25 m radius of the nest-box was not significantly different from the proportion of oak leaves in the nest but was significantly higher than the proportion of oak bark in the nest (Fig. 6; Table 6). By contrast, the proportion of birch leaves was significantly lower than the proportion of trees but the proportion of bark was significantly higher (Fig. 6, Table 6). The proportion of beech leaves was significantly higher than the proportion of trees (Fig. 6; Table 6); no bark from beech trees was observed in any nest.

#### Effect of location on reproductive parameters

Neither the date a nest was started, nor the time spent building it (Additional file 1: Table S7), was affected

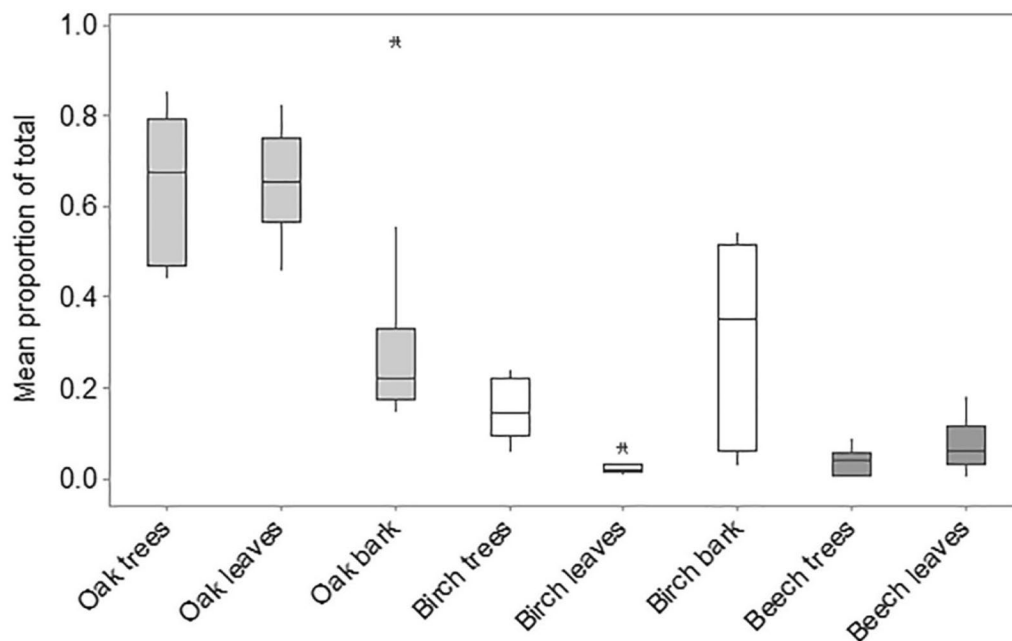




**Table 5** Results of two analyses of covariance to test the effect of tree species (tree) and nest part (i.e. cup lining or outer nest), with latitude and longitude as covariates, on the mass of leaf from the four commonest tree species, and bark from four commonest plant species found in nests (see Fig. 5)

Source	Leaf ( $R^2 = 49.1\%$ )		Bark ( $R^2 = 10.2\%$ )	
	df	F value (p value)	df	F value (p value)
Latitude	12,575	3.13 (0.077)	1,2575	3.68 (0.055)
Longitude	12,575	9.59 (0.862)	1,2575	2.67 (0.103)
Tree	12,575	23.91 (< 0.001)	3,2575	7.04 (< 0.001)
Nest part	32,575	1.19 (0.275)	1,2575	5.08 (0.024)
Latitude × longitude	12,575	3.04 (0.081)	1,2575	2.53 (0.112)
Latitude × tree	32,575	22.45 (< 0.001)	3,2575	6.97 (< 0.001)
Latitude × nest part	12,575	1.31 (0.252)	1,257	5.00 (0.025)
Longitude × tree	32,575	21.88 (< 0.001)	3,2575	5.24 (0.001)
Longitude × nest part	12,575	1.85 (0.174)	1,2575	4.53 (0.033)
Nest part × tree	32,575	73.59 (< 0.001)	3,2575	2.26 (0.079)
Latitude × longitude × tree	32,575	21.40 (< 0.001)	3,2575	5.22 (0.001)
Latitude × longitude × nest part	32,575	1.85 (0.174)	1,2575	4.51 (0.034)

The model included box area ( $\text{cm}^2$ ) as a covariate to control for variation in box size between locations. Bark masses were  $\text{Log}_{10}$ -transformed prior to analysis. Model reflects sequential model reduction by removal of non-significant higher order interactions

**Fig. 6** Box and whisker plot showing the mean of the mean proportions of each tree species within a 25 m radius of the tree on which the nestbox was attached, and proportions of leaves and bark found in the entire nest of the equivalent species. Data are from eleven different locations for which tree species were recorded. Note that no beech bark was identified in any nest

by geographical location (Table 7) but the date of clutch initiation showed a significant effect of longitude but not latitude; clutch initiation was progressively later moving from west to east (Table 7, Fig. 7). However, both latitude and longitude correlate with mean

values for clutch initiation date ( $\rho_{13} = 0.665$ ,  $p = 0.007$ ;  $\rho_{13} = 0.545$ ,  $p = 0.036$ , respectively) but not with clutch size ( $\rho_{13} = -0.351$ ,  $p = 0.199$ ;  $\rho_{13} = 0.248$ ,  $p = 0.372$ , respectively). Clutch size was also significantly greater moving eastwards but was unaffected by latitude (Fig. 7,

**Table 6** One-sample *t* values (*df*=10) comparing the difference in proportions for tree species in a 25 m radius of a nestbox with the proportion of leaf or bark of that species in the nest (Fig. 6)

Comparison	<i>t</i> ( <i>p</i> value)
Oak leaves	− 0.13 (0.901)
Oak bark	5.49 (<0.001)
Birch leaves	− 6.72 (<0.001)
Birch bark	− 3.20 (0.009)
Beech leaves	2.67 (0.024)

No beech bark was identified in the nests

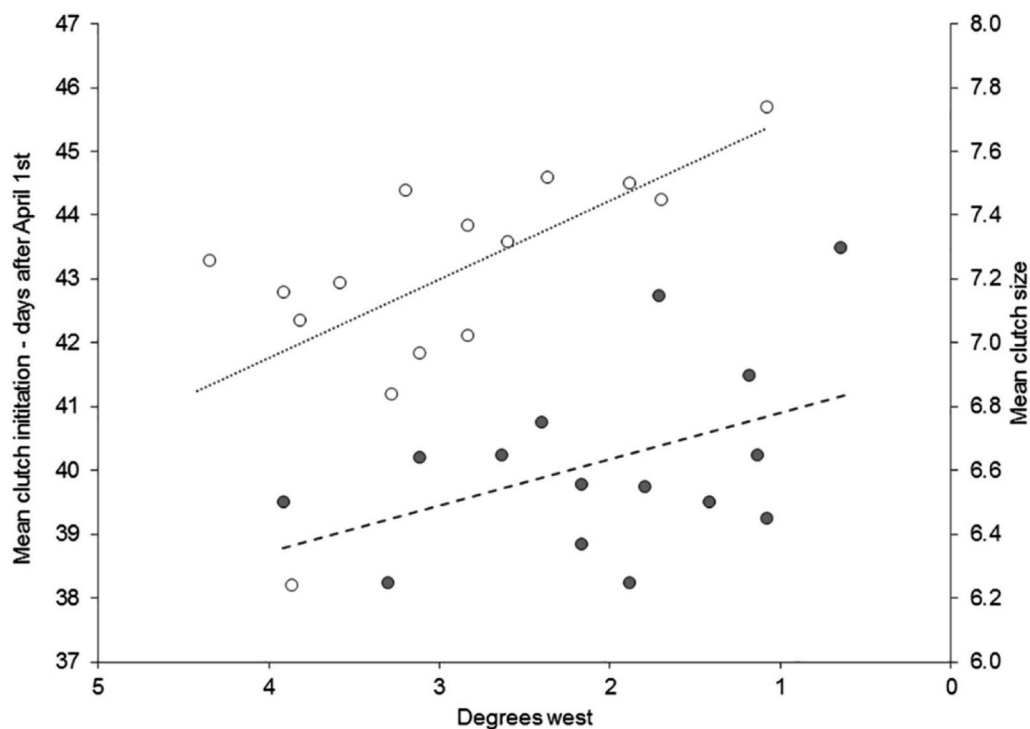
Table 7). Percentage hatchability or percentage fledging rate (of clutch size) were unaffected by geographical location (Table 6 and Additional file 1: Table S7).

## Discussion

These results indicate that there is geographical plasticity in nest composition in the Pied Flycatcher. For ‘bulk’ materials, for example leaf or moss, there was an effect of latitude and longitude. For less commonly used materials there was more geographically localised use in the nest. Only the base thickness of nests showed any effect of geographical location and whilst the date of clutch

initiation was affected by latitude and longitude other reproductive parameters were not.

Cup depth reported here was around half that reported for Pied Flycatcher nests and those of other *Ficedula* species (3.5–4.5 cm; Cramp and Perrins 1993) but cup diameter was greater. Similarly nest height and base thickness are generally smaller (about 60% and 50%, respectively) in this report than reported in the literature for the Pied Flycatcher and the Semi-collared Flycatcher (*Ficedula semitorquata*; Cramp and Perrins 1993). Nest masses reported here were generally less than reported previously (25–35 g; Stjernberg 1974; Cramp and Perrins 1993). Nest dimensions were largely unaffected by geographical location and whilst statistically significant the effect of longitude and latitude on nest cup diameter is very small (1–2 mm) and is considered as not being biologically relevant. However, the differences in base thickness may reflect a more functional relationship because base thickness increased with increasing latitude and in more easterly sites, although intraclass correlation coefficients suggested that there was high between-individual variation at any location. Presumably this reflects the cooler climate in these areas (see data cited by Mainwaring et al. 2012, 2014 that cover a broadly similar geographical range) and the thicker base would provide better insulation from below (Tiainen et al. 1983;



**Fig. 7** Relationship between degrees west and mean clutch initiation day (open circle) and mean clutch size (filled circle). Trendlines were generated by Excel

**Table 7 Results of several analyses of covariance to test the effect of latitude and longitude on various reproductive parameters**

Reproductive parameter	Latitude	Longitude	R <sup>2</sup>
Nest initiation	2.45 (0.119)	2.41 (0.122)	3.01
Clutch initiation	0.66 (0.417)	8.84 (0.003)	4.88
Nest building	1.63 (0.203)	1.95 (0.164)	0.84
Clutch size	3.28 (0.071)	6.54 (0.011)	2.37
%Hatched	0.48 (0.489)	2.17 (0.142)	0.74
%Fledged	0.50 (0.482)	3.14 (0.078)	1.07

Non-significant interaction between latitude and longitude was removed from the model, which was run again. The parameter in each row was tested individually. Percentage hatchability and fledging were arc sine h transformed prior to analysis. Values are *F* statistics, with *p* values in parentheses. Degrees of freedom = 1291 in each model

Rohwer and Law 2010; Crossman et al. 2011; Deeming et al. 2012). However, more data on climatic conditions are required to support this hypothesis. Although differences in nest dimensions may reflect geographical location (Rohwer and Law 2010; Crossman et al. 2011), there remains a general lack of information on the factors affecting variability in nests (Deeming and Mainwaring 2015).

General linear modelling suggested that longitude, but not latitude, was observed to significantly affect clutch initiation date and clutch size in the Pied Flycatcher nests although individually both correlated with clutch initiation date but not clutch size. Previous analyses have shown that altitude (up to 1900 m) and latitude (range from 34° to 69°) significantly affected clutch initiation date and clutch size in Pied Flycatchers in the western Palearctic but did not investigate the effects of longitude (range from 4°W to 29°E) because of the correlation with latitude (Sanz 1997). Re-analysis of these data for locations up to 300 m in altitude, so matching the elevation of current locations, showed that there was a significant effect of both latitude and longitude on clutch initiation date ( $p < 0.001$ ) but not clutch size ( $p > 0.05$ ). Data reported here would fall within these general patterns although the date of clutch initiation does seem to be more influenced by longitude than latitude but differences are of the order of only 3–4 days. Of course changes in clutch initiation date over the past few decades have been significantly influenced by climate change (Winkel and Hudde 1997; Both et al. 2004).

The composition of the nests reported here are similar to those previously reported for the Pied Flycatcher with the same six components being prominent (see Briggs and Deeming 2016). In addition, the geographical variability in nest composition reported between Wales and Lancashire (Briggs and Deeming 2016) is repeated but

a much wider scale. The amounts of leaves, bark and moss in the nests were inter-related with more amounts of moss being associated with less amounts of the other two but amounts of bark and leaves were positively correlated. This pattern was also observed by Briggs and Deeming (2016) for nests from Lancashire. The types of materials present in Pied Flycatcher nests in Finland were very similar although the mass of each material was not quantified (Stjernberg 1974). On a broader scale it was clear that there was intra-species variability in nest composition both between geographical sites and also at each site. In particular, Pied Flycatchers in the present study did not appear to select bark from different tree species on the basis of availability with birch apparently being preferred, and beech leaves seemed to be selected more, and birch leaves selected less, compared to their potential availability in the habitat. This result contradicts the findings of Briggs and Deeming (2016) but this probably reflects the much larger sample size from a very much larger geographical area. This kind of evidence supports the view that nest construction is not a random process (Biddle et al. 2017) but also goes to reinforce previous observations that nest construction is a plastic behaviour (Deeming and Mainwaring 2015). The factors driving these differences are not clear but below we discuss three possibilities that could explain the observations.

Firstly, birds are seeking out specific materials for nest construction. In Pied Flycatchers Stjernberg (1974) reported that over time the type of material brought to the nest cavity during nest construction changed. Two-thirds of all materials delivered on day one of nest construction was considered as ‘packing’ compared with only 4% at the end of nest construction. Indeed the types of materials in the outer nest and cup lining differ not only in the Pied Flycatcher (Briggs and Deeming 2016; present study) but in other species (see Deeming and Mainwaring 2015; Biddle et al. 2018a). Variability in nest materials could reflect functional differences between different geographical sites caused by differences in microclimate. Birds may be specifically selecting materials for key roles in the nest, as has been observed in the structural characteristics of woody materials used in thrush (*Turdidae*) and finch (*Fringillidae*) nests (Biddle et al. 2017, 2018b). Birds may select moss because it absorbs water (Wesołowski et al. 2002), or provides structural support (Wesołowski and Wiercholska 2018), or could trap more air in the nest walls (Deeming and Biddle 2015). These roles may be more important in the colder, and/or wetter north and west of Great Britain, where moss prevails in Pied Flycatcher nests. However, use of bryophytes in tit nests in Poland did not reflect the availability of species in the nesting locality but rather the birds seemed to be selecting the bryophyte species based on the structural



rigidity of its stem (Wesołowski and Wierzcholska 2018). Leaves and bark, used in more southerly locations, may not absorb as much water as moss (Biddle et al. unpublished) but may still provide structural support that would trap air in the nest walls. In our study the larger leaves of oak and beech may serve to provide greater bulk and/or structural support to the nest wall than the much smaller leaves of birch. Strips of bark could be collected from oak and birch trees but not beech (KBB personal observation), which implies that it was the morphology of the material that was important rather than its source. Indeed, even captive Zebra Finches (*Taeniopygia guttata*) select nest materials based on their structural properties or size (Muth and Healy 2014). Moreover, placement of materials within a nest does not appear to be random (Biddle et al. 2017, 2018b) and indeed nest structure can be species-specific (see Bocheński 1968; Kulczycki 1973; Biddle et al. 2018a). Selection of particular nest materials has been shown in captive Eurasian Bullfinches (*Pyrrhula pyrrhula*), which preferentially selected and broke off spruce (*Picea* sp.) twigs, apparently for its structural properties (Bocheński and Oles 1981). In addition, Blue Tits (*Cyanistes caeruleus*) on Corsica exhibit individual preferences for including particular aromatic plant species (Mennerat et al. 2009).

The present study is the first to demonstrate the widespread geographical plasticity of nest composition but whether this reflects differences in the functional properties of the nests is unclear. Differences in the amount of grass in the cup lining of blackbird nests from different locations did correlate with insulatory values, which in turn correlated with temperature but not rainfall (Mainwaring et al. 2014). Materials used in different parts of a nest reflect their structural properties (Biddle et al. 2015, 2017, 2018b). The results presented here reinforce the idea that plasticity in nest construction can be geographically widespread but more research is needed to investigate whether differences in the composition of nest walls have any effect on insulative or hydrological properties of the nest structure as a whole.

Secondly, the selection of less common materials may demonstrate that the birds are being opportunistic in the materials that they select. Briggs and Deeming (2016) showed that Pied Flycatchers used leaves of particular tree species in their nests based on the availability of leaves of that species outside the nestbox. Similar, Surgey et al. (2012) showed that use of artificial material by tit (Paridae) species was essentially opportunistic because it seemed to reflect the degree of exposure that individuals were exposed to the source of the materials; increased distances from the source reduced the rate of use. In the Pied Flycatcher nests described here birch bark and oak and beech leaves seem to offer features that the birds

seemed to seek out. However, the use of some materials, e.g. rush, was limited to a few sites in this study and this reflects the fact that this plant may not have been available in all locations. Similarly, the differential use of bark from a range of tree species across Great Britain may simply reflect the relative incidence of the species concerned at localised sites.

A third possible explanation of the observed variation in nest construction is that nest construction reflects a localised 'culture' in which birds are selecting materials on other criteria perhaps established genetically. Captive Zebra Finches have preferred colours for nest materials (Muth et al. 2013) and can associate breeding success with the colour of nest materials and choose between colour options for materials in subsequent breeding attempts to reflect their experiences (Muth and Healy 2011). However, the rearing environment did not seem to affect the colour choice of the male offspring raised by a father with a particular colour preference (Muth and Healy 2011). Zebra Finches do select nest materials based on their structural properties or size (Muth and Healy 2014) and Bailey et al. (2014) concluded that preference for a particular nest material is not entirely genetically predetermined because the type and amount of experience can influence a bird's choice. It is unknown to what extent most wild birds can learn from own experience of nest construction but Village Weaverbirds (*Ploceus cucullatus*) can improve the quality of their nests with experience (Collias and Collias 1984). The intraclass coefficient coefficients recorded here indicate, however, that within each location there is very little similarity between nests. This strongly implies that individuals are building quite different nests and the geographical variation in use of materials does not represent a localised 'culture' of nest construction within a population. Whether improvements in nest quality can be made with age and construction experience does, however, remain an interesting area for future research particularly in wild birds.

A final possibility is that variation in nest size, or composition may reflect the fitness or experience of the birds in the different locations. Food supplementation of Blue Tits and Great Tits (*Parus major*) during the nest construction phase affects nest construction and nest composition although the effects are mixed (Mainwaring and Hartley 2009; Smith et al. 2013). Experience of nest building has also been shown to affect nest composition in captive Zebra Finches (Muth and Healy 2011). It was not possible to assess either body condition, or age of birds, in this study because of the risk of nest abandonment if birds are caught at the nest (Kania 1992), so we are unable to dismiss this possibility. It would be interesting to investigate the more direct effect of bird quality or age on nest construction in a species, such as the Blue Tit

(Deeming and du Feu 2008), that is tolerant to handling at the nest.

## Conclusions

The present study showed that there is geographical variation in nest composition of the Pied Flycatcher in Great Britain. It would be useful to research into the extent this pattern extends across the European range of the Pied Flycatcher. In addition, it is likely that other species will exhibit such variability. Whilst our database of nest composition is improving it is necessary to better understand the reasons for such variability. In particular, much further research is required to ascertain whether variability nest composition affects any change in the function properties, e.g. thermal insulation, of the whole structure. Moreover, behavioural studies are needed to help us make the connection between selection of materials and their subsequent placement in the nest.

## Additional file

**Additional file 1.** Additional data and results cited in the text. **Table S1.** Mean (SD) nest dimensions for the different geographical locations. **Table S2.** Intraclass correlation coefficients with lower and upper confidence intervals for nest dimensions and composition. **Table S3.** Mean (SD) of materials (g) found in the total nest at each location. **Table S4.** Mean (SD) of materials (g) found in the outer nest at each location. **Table S5.** Mean (SD) of materials (g) found in the cup lining at each location. **Table S6.** Results of analysis of covariance to test the effect of latitude and longitude, and nest part, on minor nest components. **Table S7.** Mean (SD) values for various reproductive parameters of the pied flycatchers that constructed the nests at each location.

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## Authors' contributions

KBB devised the research and collected the data; LEB and DCD analysed the data; DCD prepared the first draft of the manuscript and all authors contributed to revisions. All authors read and approved the final manuscript.

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## Availability of data and materials

The datasets used in the present study are available from the corresponding author on request.

## Ethics approval and consent to participate

All nests, which are not re-used, involved in this study were collected after the end of the breeding season.

## Consent for publication

Not applicable.

## Competing interests

The authors declare that they have no competing interests.

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